

XX.—*On some Points in the Anatomy of the Species of Palæechinus (Scouler), M' Coy, and a proposed Classification.* By Prof. P. MARTIN DUNCAN, F.R.S., F.L.S., &c.

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THERE are some very well-preserved specimens of several species of the genus *Palæechinus* (Scouler), M' Coy, in the British Museum, in the Woodwardian Museum, Cambridge, and in the Museum of Practical Geology, Jermyn Street, and their study yields some very definite information upon some important points in their anatomy. Some of the specimens show the dorso-central system nearly perfectly, and others exhibit the ambulacral structures, so that the plates can be drawn and studied; portions of the jaws and teeth remain and, together with the interradian plates, are very interestingly preserved.

The Apical or Dorso-central System and its Variations.

It is evident that there is considerable variability in the construction of the apical system in species of *Palæechinus*. The largest specimen of *Palæechinus sphaericus* at the British Museum has the apical system with five large, tumid, basal plates, which are separate, and with five radial plates, which are placed between the basal plates and form with them a ring around the periproct. There is a circle of small, thick, and somewhat irregularly shaped anal plates immediately within the ring of the periproct. The basal and radial plates are large and tumid.

Another specimen of the same species has the apical system perfect, except in the anal plates. The periproct is pentagonal and is surrounded by a circle of thick, tumid, basal plates; the five radial plates are triangular and are only intercalated between the basal plates on the outside of the system, and they do not form a part of the ring or margin of the peri-

proct. It is very interesting to find this variability of the entrance of the radial plates, which is not uncommon in Mesozoic and recent species of Echinoidea, exemplified in the Palæechinoidea.

It was recorded by a late distinguished palæontologist, de Koninek, that the *Palæechini* were without radial plates to their dorso-central systems (Geol. Mag. vol. vii. p. 259, pl. vii. fig. 1). It appears now evident that the specimens studied by that able palæontologist had been subject to crush and irregular pressure, so that the radial plates were either pushed into the test or pressed away. In one of the specimens of *Palæechinus* in the British Museum one half of an ambulacrum was thus disposed of, so that an interradius is placed next to the median suture of an ambulacrum. There is a specimen of a *Palæechinus* in the Woodwardian Museum showing small radial plates partly crushed inwards.

The apical system of the largest specimen of *Palæechinus sphericus* in the British Museum has great resemblance to the system of *P. elegans* described and drawn by Baily, Geol. Mag. vol. ii. p. 44, and reproduced by R. Etheridge, Jun., in Quart. Journ. Geol. Soc. 1874, vol. xxx. pl. xxiv. In fact the differences are the apparent flatness of the system in Baily's figure and the presence of the perforations, which are obliterated in the British-Museum specimens.

It is evident that the generic diagnosis of *Palæechinus* must refer to the presence of five radial plates, which may or may not be perfectly intercalated between the corresponding basal plates. The specific diagnosis of *P. sphericus* must be altered from that of de Koninek and Lovén ('Études,' p. 41), for the absence of radial plates is accidental.

The small, thick, irregularly shaped anal plates of *P. sphericus* in no way resemble those of the Saleniidæ, nor in fact do those of *P. elegans*, as figured by Baily; there is no appearance of a "sur-anal."

The Anatomy of the Ambulacral Plates.

The specimens of several species of *Palæechinus* in the Museum of Practical Geology, in the Woodwardian Museum, and in the British Museum show the construction of the ambulacra perfectly. The following observations were made.

I. There are two vertical rows of pairs of pores throughout each side of an ambulacrum; the pores of the pairs are nearly or quite horizontal, but may be oblique, are separated by a thin convex septum placed vertically or nearly so, and there is no peripodium; the adoral pore of a pair is not near the adoral

suture of its plate on the outside of the test, and is equally remote from it when seen from within the test. The pairs alternate, are in a slightly sunken zone, and the interporiferous areas are rather wide and more or less convex. This arrangement of the pairs is seen in *P. gigas*, *P. sphaericus*, *P. intermedius*, *P. ellipticus*, and *P. Phillipsiæ*.

II. The plates of the ambulacra are very numerous and variable in shape in the same ambulacrum; in shape and arrangement they differ in the species, but there may be a great sameness in the plates of *P. gigas*. Simple primary plates, one large at the ambulacro-interradial end, and the next small there or blocked out, with or without alternate demi-plates, are the commonest, and true composite plates are very rare in all species and absolutely absent in some. A succession of similar primary plates, the pairs of pores being uniserial, is not observed in the species noticed above.

III. The ambulacral plates are low and yet very thick, and when in place present a zigzag at their interradian edges—there being a vertical series of alternate salient and reentering angles there, the one being at the edge of the plates which are perforated by the pairs of pores of the outer vertical row, and the other corresponding more or less to the plate of the inner row of pairs of pores. The projection of the salient angles towards the interradia is very decided as a rule, and may be more or less rounded (figs. I., II., V., VIII., X.).

This ambulacro-interradial line of suturing of course brings the zigzag of the ambulacral edge in contact with the ambulacral edge of the interradium, and this will be found to be a zigzag, and its reentering angles fit the salient angles of the ambulacral edge. Isolated plates may be seen showing these projections and depressions, and it is evident that the plates of the test were readily separable at this suture, for the ambulacra are often displaced, the ambulacral plates of the interradia being more prominent or the reverse than the ambulacra. When the opposed edges of the two series of plates are in their normal condition, the more or less rounded outer angles of the ambulacral plates are very visible and never assume the simple character figured by M'Coy and reproduced by R. Etheridge (Quart. Journ. Geol. Soc. vol. xxx. pl. xxiv. fig. 2, from M'Coy, Synop. Carb. Foss. Irel. pl. xxiv.). There is no overlap of the interradia over the ambulacra, and the test was as rigid there as in an *Echinus* and not very unlike one in the suturing.

The Ambulacra of Palæechinus gigas (fig. I., p. 206).—These

are long and narrow, and are composed of a vast number of small, low, thick plates. The vertical rows of pairs of pores are in slightly depressed poriferous zones, the interporiferous areas are slightly convex and broad, the sutures between the plates are usually distinct. The surface of a plate of some size is granular around the pair of pores and has three horizontal rows of very small, distant, primary tubercles, which have a flat circular scrobicule and a small boss; granules are also present; the minute ornamentation contrasts with the dimensions of the test. The ambulacral plates are of two kinds (*a* and *b*), each being perforated by a pair of pores near its outer end. One kind of plate (*a*) is low, broad, thick, occupies much of the interporiferous surface of the ambulacrum, and is perforated by a pair of pores not very close to the ambulacro-interradial suture; it is a plate of the inner vertical series of pairs of pores. These plates may be perfect or imperfect primaries. In the first instance (fig. I., *a*) a very low and often almost linear part is seen external to the pair of pores and reaching the reentering angle of the ambulacro-interradial suture. The low part is so small that it permits the large-ended plates of the outer vertical series of pairs of pores (*b*) to come nearly close together. In the other instance the outer linear projection of the plate has been lost (fig. I., *a'*), and the plate ends in a point, which does not reach the edge of the ambulacro-interradial suture; the linear part has been jammed out by the increasing growth of the plates of the outer series. (Fig. I., *a*, perfect primary, *a'*, a primary blocked out from the ambulacro-interradial suture.) Both kinds of plates form geometrical figures at the median suture of the ambulacrum, are highest there, and their horizontal or transverse sutures are distinct for one third or one half of the distance from the median line outwards. The existence of the second kind of ambulacral plate (fig. I., *b*), which carries a pair of pores of the outer vertical series, prevents the transverse sutural line being continuous to the ambulacro-interradial edge.

The second kind of ambulacral plate (fig. I., *b*) is perforated by an outer pair of pores, and its outer edge forms the salient angle at the suture already noticed. The plates of this kind, although large externally, are smaller than the others, are placed alternately with them, are narrow internally, and do not reach the ambulacral median line. They are low, inward-pointed demi-plates with a large outer end, where the pores are. The outer and large ends of these demi-plates are often so close vertically that, as has been already noticed, they occlude the outer process of some primary plates

(a'). It does not appear that this demi-plate and its actinal or abactinal primary ever form a true composite plate. There is no overlap of the ambulacral plates.

Lovén ('Études,' 1874, p. 41) notices *P. gigas*. He observes that the figure given of it by M'Coy (*op. cit.* pl. xxiv. fig. 4 c) shows ambulacral plates each with two pairs of pores; this he properly considered to be erroneous. W. Keeping (Quart. Journ. Geol. Soc. 1876, vol. xxxii. pl. iii. figs. 12, 13) gives M'Coy's figure and a correction. Now, although these drawings show a marked difference from the structures visible in the specimens I have described, still in specimens where obliteration of the sutures has taken place and where the pores are greatly crowded vertically, both of the appearances drawn by M'Coy and Keeping are to be recognized. But they are deceptive, and the truth is explained in weathered parts of the same test. Nevertheless there were no intercalated demi-plates noticed in M'Coy's definition of the genus or species. Lovén places *P. gigas* in a group of *Palæechini* which have the ambulacral plates differing alternately, having the same height at the median suture and one entire (a primary), and the other reduced to a cuneiform demi-plate, its point directed outwards. In the specimens of *P. gigas* in London and Cambridge the demi-plate has its point directed towards the median line, which it does not reach. It will be seen, however, that the structure noticed by Lovén is found in another species, *P. sphaericus*.

Ambulacra of *Palæechinus ellipticus* (fig. VIII.) present ambulacral plates somewhat similar to those of *P. gigas*, and the pairs of pores are biserial on each side of an ambulacrum. Hence there is an error in the specific diagnosis and drawing of M'Coy (in Foss. Mount. Limestone Ireland, 1842, pl. xxiv. fig. 3; *P. gigas* is incorrectly drawn, fig. 4).

The specimen in the Museum of Practical Geology (XIII | $\frac{2}{30}$) shows very convex interporiferous areas. The plates with the outer pairs of pores are small demi-plates; the primary plates with the inner rows of pairs of pores are narrowed between the demi-plates and usually do not reach the ambulacro-interradial suture (fig. VIII.).

Ambulacra of *Palæechinus sphaericus* (figs. II.—VII.).—There are two specimens of this species, one a crushed mass and the other more or less prolately spheroidal, in the British Museum which show the structure of the ambulacra very well. The arrangement of the pores in two vertical rows of

pairs is the same as in *P. gigas*, but the shape and the nature of the plates differ. The commonest arrangement of the plates is seen at a little distance from the apical system (fig. II.). The pores of the pairs, which are in two vertical series and alternate, are large and often rather broad; they are separated by a septum, as in the other species. As in *P. gigas*, the pair of pores of the outer vertical row (*b*) are in plates which form the salient angle of the zigzag at the ambulacral edge; and the pair of pores of the inner row (*a*) are in relation with the reentering angles. The plates are of two principal kinds, and the first to be noticed are those which are perforated by the inner pairs of pores. These plates are either perfect, low, broad primaries, highest at the ambulacral median line (*a*), having much transverse suture, and narrowing and becoming pointed at the ambulacro-interradial suture, or imperfect primaries, with their outer part, near the ambulacro-interradial edge, reduced to a point which does not reach outwards to the outward edge (*a'*). Both of these plates are usually high at the median line and have a single horizontal row of minute scrobiculate tubercles, with a boss and some granules (fig. II., *a, a'*).

The other principal kind of plate (fig. II., *b*) is a low primary, as broad as those just described, but slightly lower at the median line and larger externally, where there is a large pair of pores of the outer vertical series. The plate is expanded around the pores and highest there. The ornamentation is the same as that of the other plates. It will be observed that this arrangement is different from that of *P. gigas* and that both plates are primaries, there being no demi-plate. Nearer the apical system the size of the pair of pores is not sufficient to produce much enlargement of the outer part of the plate, which has an outer pair of pores (fig. III., *b*). But the slight increase of height is readily seen, and it has the effect of diminishing the size of the next plate (*a*), with an inner pair of pores (fig. III.). It certainly appears, when the sutures of the plates are invisible, as if there were two pairs of pores to a plate, as M^cCoy drew and Keeping criticized.

One composite plate is seen in a specimen near the apical system and the components are primaries; the inner edge of the combined plates forms an angle, and the larger plate is with a large outer and inner part (fig. IV., *b*), while the smaller plate (*a*) is low at both ends and has a suture curved adorally.

A common arrangement of the plates of the ambulacra (fig. V.) is as follows:—

A plate (fig. V., *b'*) is large where it is pierced by the pores, and forms a projecting angle at the ambulacral edge;

it is broad, and whilst its height is the same as that of the other plates at the median ambulacral line, it is nipped in, vertically, at its middle in consequence of the shape of the plates above and below it (a^1 and a^2). The first of these (a^1) is a low primary, smallest at the extremities, pierced by an inner pair of pores, and it has a transverse curved adoral edge and also a convex aboral sutural edge to connect it with the primary (b').

The other plate, a primary (a^2), is aboral to the primary b' , is tall at the ambulacral median line, low close to the pair of pores, and externally it is not quite reduced to such a mere point as in the instance of the first component (a^1), which just reaches the ambulacro-interradial edge at a reentering angle. The adoral sutural edge of the plate (a^2) is convex and the aboral edge is straight or slightly concave in the opposite direction. The arrangement of these three unequal primary plates has geometrical outlines neither externally nor at the median ambulacral line, and is repeated in the vertical succession (fig. v., a^1, b, a).

Amongst the plates of this species are some which are not only characteristic but very suggestive of the reduced and isolated plates of other Palæchinoidea and of the later Echinothuridæ.

A composite plate (fig. vi.) has a small aboral primary a and a large middle primary b ; but the third component is adoral and at the ambulacro-interradial edge, and is a small demi-plate looking like a peripodium without a plate, and it is crushed a little out of place. This demi-plate (a') should be compared with that seen in a doubtful composite plate (fig. vii., a'). It is evident that the crush of growth has enabled the large primary plate (b^2) belonging to the outer vertical row of pores to crowd out, with the assistance of its adoral neighbour (b^1), the primary of the inner row. This has lost all its inner part, has become a demi-plate (a'), and but a trace of the outer portion remains; the rest is like a thick peripodium.

The occurrence of small isolated plates along the lines of transverse sutures, a phenomenon especially Echinothurian in the recent fauna, has therefore a certain explanation. The plates thus placed and small are not additional and intercalated plates, but are the results of growth, crowding, crushing out and in, and atavism of original plates.

It does not appear unreasonable to account for the presence of four vertical rows of ambulacral plates in some Palæchinoidea by an early movement of the plates perforated by the inner row of pairs of pores inwards whilst the growth proceeded.

The thickness of the ambulacral plates of *P. gigas* and *P. sphericus* is remarkable, and is much greater than their vertical height; there is no overlap of the edges and the test was rigid.

The interradial plates of the species are very thick and the edges present no evidence of flexibility. The ambulacral rows of plates have their ambulacral edges as zigzags and the angles fit into the corresponding reentering angles of the ambulacral plates. The resemblance to many Mesozoic and recent species of regular Echinoidea is exact in this respect.

Ambulacra of Palæechinus intermedius, W. Keeping (Quart. Journ. Geol. Soc. vol xxxii. p. 37, pl. iii. figs. 9-11).—There are specimens of this species in the Woodwardian Museum and also in the Museum of Practical Geology. The late Mr. W. Keeping doubted whether the species could be placed with *Palæechinus*; but he was misled, apparently, by the diagnosis of M^cCoy, especially of the part relating to the construction of the poriferous zones. The ambulacra of *P. intermedius* have biserial pairs of pores and the plates are very numerous, low, broad, and thick (figs. IX. and X.). The plates are all primaries and are in regular vertical succession, so that there is a single vertical row of them on each side of the median ambulacral suture. But the plates are different in shape in the same vertical row, although not to the amount shown in *P. gigas*. The plates with the outer pairs of pores are largest at their outer part, which forms the salient angle of the ambulacral edge of the ambulacro-interradial suture, and they reach the median ambulacral line, being lower there than near the part which bears the pair of pores. The plates which bear the inner series of pairs of pores are narrow externally and may or may not reach the interradial suture, and if they do so it is by a pointed angle. They are low, broad, and are often higher at the ambulacral median line than the other primaries with the outer series of pairs of pores. Fig. IX. from a specimen in the Museum of Practical Geology and fig. X. from the Woodwardian specimen.

Ambulacra of Palæechinus Phillipsiæ, Forbes.—*Palæechinus Phillipsiæ*, Forbes, is to be seen in the form of models which have been made by running in a melted substance into the hollow fossil. This substance, when solid, shows the inside of part of the test, and therefore the ambulacral and other plates are represented on the model so far as their inner surfaces are concerned.

The model at the Museum of Practical Geology shows a double row of pairs of pores here and there, in an ambulacrum, but the suturing of the plates is not visible. Nevertheless the plates were evidently arranged after the system of the primaries of *P. sphericus* (fig. II.). Forbes gives a diagram of the plates and the pairs; but the inner pair of pores is placed too close to the median line of the ambulacrum and its plate is too much blocked out from the ambulacro-interradial suture. (Compare Forbes, 1848, Mem. Geol. Survey United Kingdom, vol. ii. pt. i. p. 384, pl. xxix. fig. 1, and the fig. II. of this communication.)

The Grouping of the Species.—It will have been observed that no less than five species of *Palæechinus* present two vertical rows of pairs of pores on each side of the ambulacra. The species group themselves into two divisions. In one, containing *P. gigas* and *P. ellipticus*, the outer pairs of pores of the vertical rows are in demi-plates, and in the other division, containing *P. sphericus*, *P. intermedius*, and *P. Phillipsie*, the plates of both sets of pairs of pores are primaries, some being blocked out from the ambulacro-interradial sutures. Very rarely there is some crowding and union of plates to form compound ones, as in *P. sphericus*.

It is very remarkable how distinct some of the plates are from their neighbours, and it is evident that their great thickness would keep them from overlapping. It would seem at first sight as if there had always been a space between the edges of the plates; but in the Woodwardian specimens and in some elsewhere the plates are often so close that there is no vestige of a sutural line between them. Hence the drawings given by M'Coy and W. Keeping, which have been noticed.

The Characters of Palæechinus elegans and P. quadriserialis.—The question arises, Where are *Palæechinus elegans*, M'Coy, *P. quadriserialis*, J. Wright (Journ. R. Geol. Soc. Irel. vol. i. p. 62, pl. iii.), and a small-plated *Palæechinus* in the Woodwardian Collection, which does not present the characters of any of the five species mentioned above, to be placed?

In a classification of recent or Mesozoic Echinoidea no one would place species with a single vertical row of pores on each side of an ambulacrum in the same genus as species presenting two vertical series of pairs on each side of an ambulacrum, the plates differing markedly in their shape and arrangement also. *Cidaris* is separated on these lines from *Diplocidaris*. Now *P. elegans* has all its ambulacral plates

and primaries subequal, and there is no crowding to form demi-plates or to crush out parts of plates from the interradial sutures. The plates are Cidaridean in their simplicity and each has a pair of pores, so that there is one vertical series on each side of an ambulacrum. This is the case with *P. quadriserialis* and with the small *Palæechinus* in the Woodwardian Museum. It must be admitted that the alliance is close, but these species cannot enter the same genus as *P. gigas* for instance. Unfortunately M' Coy was not impressed with the value of the ambulacral characters, and placed *P. gigas*, *P. elegans*, *P. ellipticus*, *P. sphericus* and another as types of his genus *Palæechinus* (M' Coy, in Griffith, Foss. Carb. Limest. Irel. 1842, p. 171, see pl. xxiv.), every ambulacrum being wrongly figured by his artist. W. Keeping was clearly impressed with the want of homogeneity in the genus; and when he met with the specimen in the Woodwardian Museum, which has a small test with small plates and straight, single, vertical rows of pairs of pores, one series of pairs only being found upon each side of an ambulacrum, he defined a new genus *Rhoechinus* (*op. cit.* p. 37). Really this genus, with a very slight modification, will embrace the forms of *Palæechinus* with uniserial pairs of pores.

From our present knowledge, if *Palæechinus* is to remain as a genus—and it ought to do so, for M' Coy's work claims great respect—it must be as *Palæechinus*, M' Coy (*pars*), and relate to species with a double vertical row of pairs of pores, such as *P. gigas* and *P. sphericus*. *Rhoechinus*, Keeping, slightly modified, will then contain *P. elegans*, possibly *P. quadriserialis*, and certainly the little form in the Woodwardian Museum.

Synonymy.

Genus PALÆECHINUS, M' Coy, *pars*.

P. gigas, *P. sphericus*, *P. ellipticus*, *P. intermedius*,
P. Phillipsiæ.

Genus RHOECHINUS, Keeping.

R. irregularis, Keeping; *R. elegans*, M' Coy, *sp.*; *R. quadriserialis*, J. Wright, *sp.*; *R. sp.* (in the Woodwardian Museum, named a *Palæechinus*).

The two North-American species, which I have not seen,
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appear to belong to *Palæechinus* as now limited. *P. Konigii*, M' Coy, is insufficiently diagnosed, the type being fragmentary.

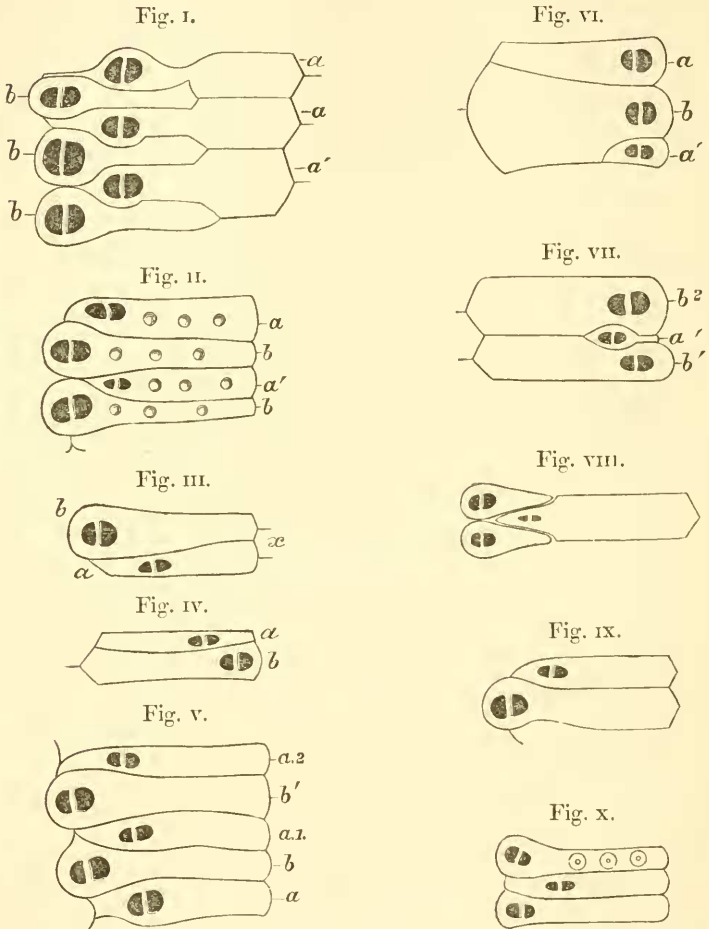


Fig. I.—One side of part of an ambulacrum of *Palæechinus gigas*, magn.
 Figs. II.-VII.—Plates of part of one side of ambulacra of *P. sphaericus*, magn.
 Fig. VIII.—Two demi-plates and a blocked-out primary of *P. ellipticus*, magn.
 Figs. IX., X.—Parts of one side of an ambulacrum of *P. intermedius*, magn.

The obliquity of the pores of the pairs is sometimes not with the adoral pore directed more or less actually; this unusual condition is represented in figs. II., V., VI., and IX.